

Winter feeding ecology and trophic relationships of Oldsquaws and White-winged Scoters on Kachemak Bay, Alaska

by Gerald A. Sanger and Robert D. Jones, Jr.
US Fish and Wildlife Service, 1011 East Tudor Road,
Anchorage, AK, USA 99503

1. Abstract

The feeding ecology of Oldsquaws (*Clangula hyemalis*) and White-winged Scoters (*Melanitta deglandi*) was studied on Kachemak Bay from November 1977 through April 1978. These species form the bulk of a large wintering waterfowl population. Oldsquaws were extreme generalists, eating at least 61 prey species. The most important were the Pacific sand lance (*Ammodytes hexapterus*), Stimpson's surf clam (*Spisula polynyma*), and blue mussel (*Mytilus edulis*). Scoters were generalists on molluscs, mostly bivalves. They ate at least 22 prey species; the most important were the common Pacific littleneck clam (*Protothaca staminea*), blue mussel, and puppet margarite snail (*Margarites pupillus*). There was little overlap in kinds of prey between the two ducks, and when it occurred the scoters ate significantly larger prey. On the basis of birds observed and collected and the known habitats of their prey species, both sea ducks presumably foraged in water less than 20 m deep. Oldsquaws mostly over substrates of sand and mud, and scoters mostly over bottoms of shell debris and cobbles. The base of the food web in Kachemak Bay depends on the production and availability of organic detritus. Little is known about ecological processes between production of detritus and the production and availability of the birds' filter- and deposit-feeding prey. However, both ducks apparently function as first- to fourth-order carnivores, depending upon which prey species they eat.

2. Résumé

De novembre 1977 à avril 1978, nous avons étudié l'écologie alimentaire des Canards kakawis (*Clangula hyemalis*) et de la Macreuse à ailes blanches (*Melanitta deglandi*) dans la baie de Kachemak. Ces espèces forment la majeure partie de la vaste avifaune hivernante. Les Canards kakawis ont un régime extrêmement opportuniste, comprenant au moins 61 espèces. Les plus importantes étaient : le lançon gourdeau (*Ammodytes hexapterus*), la palourde de Stimpson (*Spisula polynyma*) et la moule bleue (*Mytilus edulis*). Les macreuses se nourrissent indifféremment de mollusques, surtout de bivalves. Leur régime se composait d'au moins 22 espèces. Les plus importantes étaient : le protothaca du Pacifique (*Protothaca staminea*), la moule bleue et la margarite pupille (*Margarites pupillus*). Nous avons constaté très peu de concurrence pour les espèces consommées entre les deux canards, mais, le cas échéant, les macreuses capturaient des proies significativement plus grosses. Si on en juge par les oiseaux observés et recueillis et les habitats connus de leurs proies, ces deux canards de mer puiseraient leur nourriture

à des profondeurs inférieures à 20 m : les Canards kakawis, dans les eaux couvrant des substrats de sable et de boue, et les macreuses, sur des fonds de débris de coquillages et de cailloux roulés. Le réseau trophique dans la baie de Kachemak repose sur la production et la disponibilité de détritus organiques. Nous savons très peu de choses sur les processus écologiques intervenant entre l'accumulation de détritus et la production et la disponibilité des proies se nourrissant par filtration ou de dépôts. Nous savons cependant que ces deux canards agissent apparemment comme carnivores de premier à quatrième ordre, tout dépendant de l'espèce de proie qu'ils consomment.

3. Introduction

Kachemak Bay, near the mouth of Cook Inlet in southcentral Alaska (Fig. 1), has high biological productivity, and important commercial fisheries and recreational uses (Trasky *et al.* 1977). Erikson (1977) conducted surveys of marine birds on the bay in 1976 as part of broad-based environmental studies of adjoining Cook Inlet (Trasky *et al.* 1977). He discovered that over 90% of the marine birds in lower Cook Inlet in winter were in Kachemak Bay and that most of these were waterfowl. J.H. Crow (unpubl. data) studied the foods of marine ducks shot by hunters in the China Pool Bay area of Kachemak Bay during September–November 1977, and David Erikson (unpubl. data) collected sea ducks for food studies in spring 1976 in the inner bay. The feeding habits of wintering birds remained essentially unknown, however.

In order to fill this gap, we studied the feeding ecology of the main species of marine-associated birds wintering on the bay. The primary objectives were to determine the kinds, amounts, and trophic levels of prey used by the main species of birds and to relate these findings to the physical and biological environment of the bay. A secondary objective was to make general observations of the distribution and feeding behaviour of the birds. This paper concerns the feeding ecology of the two main species of sea ducks, the Oldsquaw (*Clangula hyemalis*) and White-winged Scoter (*Melanitta deglandi*). Other species of waterfowl were present, but none were consistently present in areas that we could reach safely in our open skiff.

4. Description of study area

Kachemak Bay is a major geographic feature of the Kenai Peninsula and Cook Inlet in southcentral Alaska (Fig. 1). It is 38 km wide at its entrance and about 62 km long. Homer Spit projects 7 km into the bay, dividing it into

physically and biologically distinct "inner" and "outer" bays. The north shore of the bay is unbroken by inlets, but the south side has several islands, fiords, and shallow bays. The mean diurnal tide range is 4.7 m (Trasky *et al.* 1977).

In the inner bay, scattered boulders occur on extensive mud flats immediately adjacent to shore and on the sand and mud bottom just beyond (Fig. 1) (Lees and Driskell 1981). Blue mussels (*Mytilus edulis*) and other biota encrust the boulders, which thus constitute rocky microhabitats. Clays originating from glacial streams at the head of the bay and from erosion of bluffs extend from there to a depth of 18 m.

In the northern outer bay, areas shallower than 9 m are more subject to tidal currents than those in the inner bay, and substrates are markedly different. Boulders and cobbles predominate in depths less than 18 m. From there to the 37-m depth contour the substrate is shell debris, muddy sand, or rippled sand. Water depths away from shore in both the inner and outer bays range mostly from about 35 to 90 m.

Most water in Kachemak Bay originates from coastal upwelling just off southernmost Kenai Peninsula (Burbank 1977, Trasky *et al.* 1977). Surface water flows into the south side of the outer bay from Cook Inlet, and a net northwest current flows out of the bay along the north shore. Droque studies suggest that the same water can remain in the outer bay for several days before moving out of it (W.P. Wennekens, pers. commun.). Water enters the inner bay from the outer bay at subsurface depths and from streams at the head of the bay. Circulation patterns directly influence the transport of mineral sediments and organic detritus, and sedimentation affects substrate type and thus the nature of benthic animal communities. Organic detritus is believed to form the base of the Kachemak Bay ecosystem (Lees and Driskell 1981).

Ice can build up considerably in the shallow inner bay behind Homer Spit. During this study we encountered

moderate amounts of pan and brash ice from December to March in the inner bay between the spit and Fritz Creek (Fig. 1). Ice scouring of the bottom can adversely affect the benthos (Lees and Driskell 1981), thus directly influencing the distribution of the birds' prey. Air temperatures in winter are generally below freezing; during this study they ranged from -13°C in December to 4°C in April. Surface water temperatures generally ranged from 4 to 5°C .

5. Methods

5.1. Field methods

We collected birds for stomach samples from a 5-m open skiff during monthly field trips of 3–5 days duration from November 1977 through April 1978. We also recorded general observations of the birds' distribution and behaviour. We worked on the north side of the bay and generally stayed on the lee side of Homer Spit during adverse or threatening weather. Birds were collected only if they were sitting on the water. We often saw Oldsquaws actively diving (and presumably feeding) in the shallow inner bay before collecting them, but we never observed the generally wary scoters do so. Immediately after collection we injected the stomachs of specimens with 10% buffered Formalin to arrest digestion (van Koersveld 1950). Specimens were then frozen until laboratory processing.

We collected 28 Oldsquaws, including 5 each month from November through February in the inner bay, 6 in March in the outer bay, and 1 each in the inner and outer bays in April. We collected 39 White-winged Scoters, as follows: 1 in November and 2 in December in the inner bay, and 14 in January and 5 each in February, March, and April in the outer bay. All birds were collected within a few kilometres of the north shore of the bay at depths ranging from about 2 to 20 m (mean lower–low water).

5.2. Laboratory methods

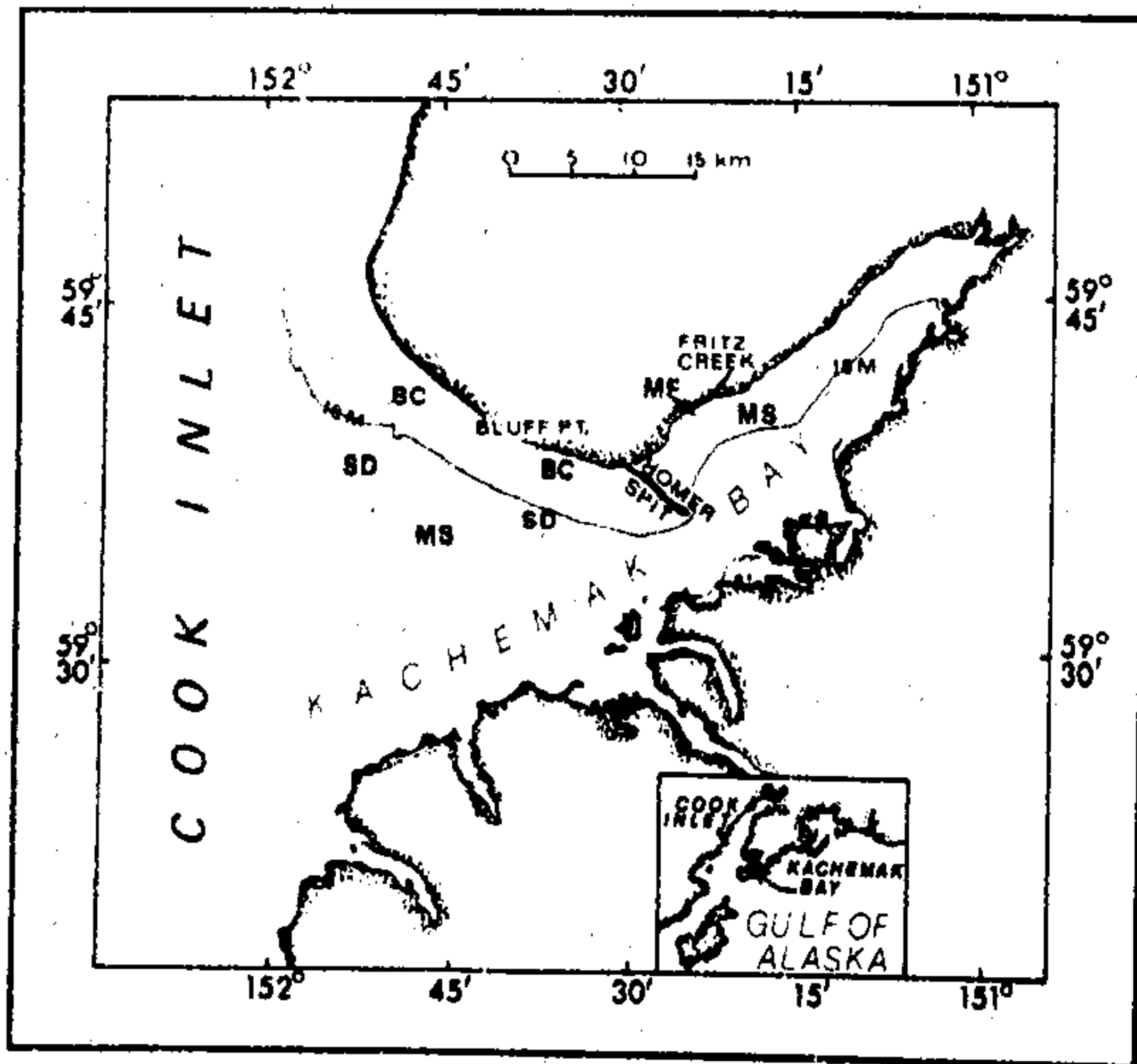
In the laboratory we recorded body weight and sex of the specimens and removed the esophagus, proventriculus, and gizzard intact. The stomach was carefully cut open, the contents drained of excess moisture, weighed to the nearest 0.1 g, and the volume measured to the nearest millilitre by water displacement. We then counted and identified the prey items to the lowest possible taxon, and visually estimated their volume as a percent of the total. The greatest length of whole specimens was measured to the nearest millimetre. All data were recorded on a standardized form.

5.3. Methods of data analysis

We used three basic parameters to describe prey taxa in the stomach samples: aggregate percent volume (cf. Martin *et al.* 1946, Swanson *et al.* 1974), aggregate percent numbers, and percent frequency of occurrence. We calculated these three parameters both for species and certain higher taxa, for individual months, and for samples pooled for the entire study. Details are reported in an administrative report (Sanger and Jones 1982) and summarized in sections 6 and 7.

Differential digestion rates of hard- and soft-bodied prey may distort their original relative volumes; percent numbers can make an abundant small prey seem more

Figure 1
Kachemak Bay, Alaska, indicating bottom substrates (Driskell and Lees 1977, SAI 1979) in areas where birds were collected (Key: BC = boulders and cobbles; SD = shell debris; MS = muddy sand; MF = mudflats)



important than a sparse larger one, and percent frequency of occurrence ignores numbers and volume. Pinkas *et al.* (1971) attempted to overcome these shortcomings by combining the three values into an Index of Relative Importance (IRI), which we use here. The IRI is defined as:

$IRI = \%FO (\%V + \%N)$, where

$\%FO$ = % frequency of occurrence of a prey taxon in a sample of n birds.

$\%V$ = % aggregate volume of a prey taxon in the combined volume of all taxa in the stomachs of the sample of n birds.

$\%N$ = % aggregate numbers of a prey taxon in the combined numbers of all taxa in the stomachs of the sample of n birds.

We characterized the feeding habitats of the birds by comparing substrate types (Fig. 1) at their collection sites with what is known about their feeding behaviour and the habitats of their prey.

As far as possible, common and scientific names of molluscs discussed below are from Abbott (1974), those of shrimps are from Butler (1980), and those of fishes are from Robins *et al.* (1980).

6. Oldsquaw feeding ecology in Kachemak Bay

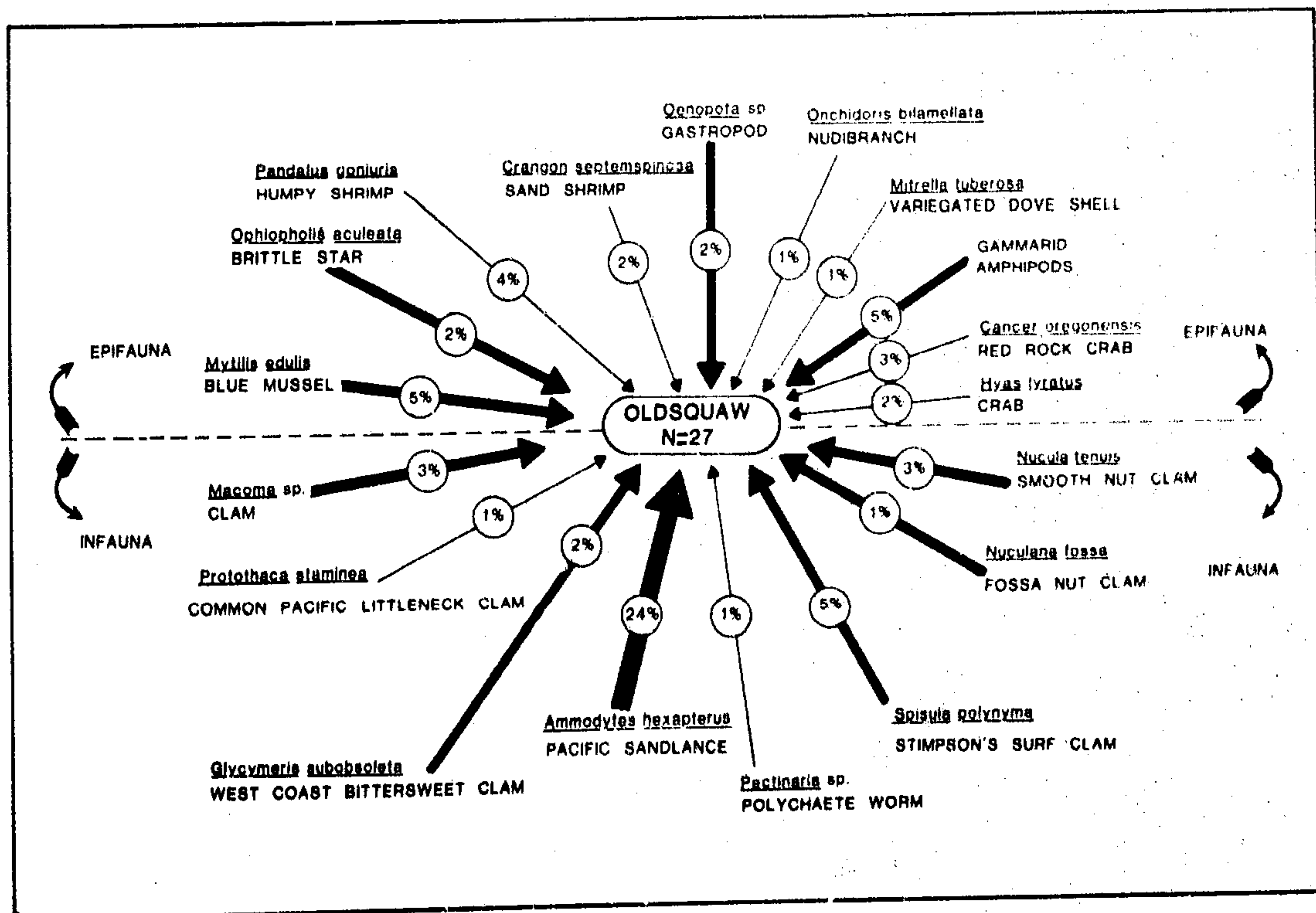
6.1. Diet of Oldsquaws

Twenty-seven of 28 birds had identifiable prey in their stomachs; the remaining bird contained only unidentified remains. Oldsquaws ate several higher taxa of prey. These included 1 foraminiferan, 9 polychaetes, 14 gastropods, 12 bivalves, 17 crustaceans (including 1 each of a barnacle, mysid, cumacean, and isopod; and at least 8 gammarid amphipods, 3 shrimps, and 2 crabs), 1 ectopod, 3 echinoderms (including 2 brittle stars and 1 sea urchin), and 2 fish. The most important higher taxa and their IRI values were bivalves, 3170; crustaceans, 1393; fish, 1168; gastropods, 523; and polychaetes, 321.

With a minimum total of 61 prey species (Sanger and Jones 1982), Oldsquaws had an extremely diverse diet. A sink food web (Cohen 1978) illustrates the relative importance of the 18 most important species of prey, based on their IRI values (Fig. 2). Only those prey with both an IRI of at least 10 and which constituted at least 1% of the volume are included. The dominating importance of Pacific sand-lance (*Ammodytes hexapterus*) is readily seen.

Figure 2

Food web for 27 Oldsquaws wintering on Kachemak Bay, showing primary kinds of prey and their respective % of total prey volume. (Only prey with an IRI of 10 or more and which constituted at least 1% of the volume are included. Arrow sizes based on IRI value of prey, as follows: small = 10-99; medium = 100-999; large = 1000-9999)



The most important taxa overall and their IRI values were Pacific sandlance, 1059; Stimpson's surf clam (*Spisula polynyma*), 935; blue mussel, 892; smooth nut clam (*Nucula tenuis*), 215; west coast bittersweet (clam) (*Glycymeris sub-obsolata*), 195; fossa nut clam (*Nuculana fossa*), 106; and the turrid gastropod *Oenopota* sp., 114. Except for sandlance, and perhaps the Stimpson's surf clam and blue mussel, it is difficult to say if these species were truly more important than many of the others. The species composition in the diet was radically different from month to month, and some higher taxa like gammarid amphipods (383) were collectively more important than most species of bivalves. Infauna made up 40% of the total volume of the prey, and it is assumed that Oldsquaws captured sandlance when they were buried in the sand (Meyer *et al.* 1979).

6.1.1. *Monthly changes in prey importance* — Small sample sizes limit statistical evaluation of monthly changes in the importance of various prey, but general trends were indicated. Fish, mostly sandlance, were present in the Oldsquaws' diet each month except February and April. Crustaceans were moderately important throughout the study, but no one species nor higher taxon was consistently important.

Other prey taxa fluctuated in their importance in no apparent pattern. A shrimp (*Spirontocaris spina*), mysids, and echinoderms (brittle stars and sea urchins) occurred only in the diet of birds collected in the outer bay during March. Bivalves and other prey displayed no monthly trends.

6.1.2. *Prey size* — Lengths of 34 prey species of Oldsquaws (Sanger and Jones 1982) ranged from 1-mm variegated lacunas (periwinkle) (*Lacuna variegata*), *Macoma* sp. clams, and blue mussels, to sandlance of 115 mm; 95% of the prey were less than 10 mm, and only 2% were over 19 mm. The mean length of 1079 measurable prey was 6.8 mm (SE = 0.33). Most of the measurable prey were gastropods ($N = 84$) and bivalves ($N = 928$).

Most bivalves were less than 6 mm, but data for *Macoma* sp. and blue mussels suggest the presence of at least a few older animals. Abbott (1974) noted 76 mm as the maximum length attained by blue mussels, so those of less than 10 mm were clearly subadults. Stimpson's surf clams, 88% of them 2–4 mm, were all age class "0" (Feder and Paul 1981).

6.2. Feeding habitats and feeding behaviour

The kinds of bottom substrates over which the birds were collected and the species and habits of their prey suggest that the Oldsquaws taken had fed benthically on both infauna and epibenthos. We observed birds mainly in the northern inner bay over mud-sand substrates, but we occasionally saw them in the outer bay over shell debris and cobble habitats.

We often saw Oldsquaws actively diving (and presumably feeding) within pan and brash ice in the inner bay behind Homer Spit. The ice probably protected the birds by shielding them from the wind and by damping the waves.

With the exception of sandlance and various species of shrimp, the Oldsquaws' prey were sessile or weakly mobile. The birds possibly captured sandlance that were buried in the sand (Meyer *et al.* 1979), although they are known to eat free-swimming fishes (e.g. Peterson and Ellarson 1977). The preponderance of sessile animals in their diets may indicate a limited adaptation for capturing quickly moving fauna, however.

Values on the weight of food in stomachs as compared with the net weight of individual birds imply that Oldsquaws did not eat large amounts of food at any one time. These values ranged from a low of 0.2% in November and February to a high of 3.0% for a bird in March (20 g of food in a 674-g bird). Average monthly values were very low, ranging from 0.45% (SE = 0.15) in April, to 1.6% (SE = 0.32) in March. The overall average for the 28 specimens was 1.0% (SE = 0.19). Sixteen birds (57%) had values less than 1.0%, but only four (14%) had values greater than 1.5%.

7. White-winged Scoter feeding ecology in Kachemak Bay

7.1. Diet of White-winged Scoters

The stomach of one specimen in February was empty, but the remaining 38 birds (97%) had food in their stomachs (there are no prey volume data for one specimen). Two other specimens collected in February 1977 as part of another project on the south side of the outer bay both contained food. Overall IRI values show that the most important major prey taxa by far were bivalves (6112) and gastropods (1510). Polychaete worms and crustaceans (16 each), and echinoderms (6) were of minor importance. White-winged Scoters had a fairly diverse diet, eating a minimum of 22 species of prey (Sanger and Jones 1982).

A sink food web of the seven main prey species (Fig. 3) illustrates the importance of blue mussels (IRI 1158) and the common Pacific littleneck (clam) (*Protothaca staminea*) (IRI 1996). These species made up 31 and 32%, respectively, of the aggregate prey volume; this contrasts to their low importance to Oldsquaws. A gastropod, the puppet margarite (*Margarites pupillus*) (IRI 151), was relatively important compared with the remaining prey, none of which had an IRI value higher than 60. Volumes of the main epifaunal and infaunal prey were about equal in the scoters' diet (Fig. 3).

7.1.1. *Monthly changes in prey importance* — Monthly sample sizes were small, but some dietary changes in birds collected were apparent. Bivalves, in particular, and gastropods were consistently important in the scoters' diet. Other major taxa were of minor importance and occurred sporadically. The blue mussel was the only prey in three birds collected in the inner bay in November and December. The common Pacific littleneck clam was consistently important to scoters collected in the outer bay from January through April, but other prey taxa were sporadic in the scoters' diet.

The two birds collected on the south side of the outer bay in February 1977 had eaten mostly the clam *Astarte rollandi* and the west coast bittersweet. Differences in prey species compared with the north side of the bay may have reflected differences in prey availability rather than prey selection.

7.1.2. *Prey size* — Lengths of 14 prey species of scoters (Sanger and Jones 1982) ranged from common northern admetes (gastropod) (*Admete couthouyi*) of 4 mm to a *Nephtys* polychaete worm of 105 mm. Lengths of 103 measurable prey pooled from all stomachs averaged 13.6 mm (SE = 1.42). Some 90% of the prey were less than 20 mm, but the occasional presence of bivalves and gastropods over 40 mm shows that scoters sometimes ate larger prey.

7.2 Feeding habitats and feeding behaviour

The kinds of bottom substrates over which the birds were collected and the species and habits of their prey suggest that the birds taken fed exclusively in benthic habitats, usually in areas with shell debris and boulder-cobble substrates, but occasionally in sand and mud. White-winged Scoters occurred relatively infrequently in the inner bay over sand-mud substrates (Erikson 1977 and this study), and the three we collected there contained only blue mussels. Thus, the scoters may have captured prey such as *Macoma* clams and arctic naticas (gastropod) (*Natica clausa*), animals typical of sand and mud (Keen and Coan 1974), in pockets of such substrates amid the shell debris and cobbles in the outer bay (Dennis Lees, pers. commun.).

The fairly wide range in prey sizes indicates that, although scoters are able to selectively eat molluscs as large as 70 mm, they probably sieve through the substrate to locate smaller prey; about half their prey were infauna. It is unlikely that much light reaches the scoters' feeding habitats, which suggests that the birds locate their food by probing the substrate with their bill and tongue, which are richly supplied with tactile nerve endings (Welty 1962:90).

The weights of food in stomachs as compared with weights of individual birds suggest that, like the Oldsquaws, White-winged Scoters ate only small amounts of food at any one time. These values ranged from zero (empty stomach) in February 1978 to a high of 4.0% for one bird each in February and March. The latter bird, weighing 1911 g, had 78 g of food in its stomach, the maximum observed. Average values from November through April ranged from 2% to 2.6%, and the overall mean for the 39 birds was 2.2% (SE = 0.16). Only five birds (13%) had values less than 1%; this, considered with the fact that only one bird had an empty stomach, suggests that the birds were consistently able to find food.

8. Comparisons between diets of Oldsquaws and White-winged Scoters

The Oldsquaws and White-winged Scoters we collected ate substantially different species of prey (cf. Figs. 2 and 3). We encountered Oldsquaws primarily in the inner bay over substrates of sand and mud, and most of the White-winged Scoters we saw were in the outer bay over substrates of cobbles and shell debris.

Figure 3

Food web for 37 White-winged Scoters wintering on Kachemak Bay, showing primary prey species and their respective % of total prey volume. (Only prey with an IRI of 10 or more and which constituted at least 1% of the volume are included. Arrow sizes based on IRI value of prey, as follows: small = 10-99; medium = 100-999; large = 1000-9999)

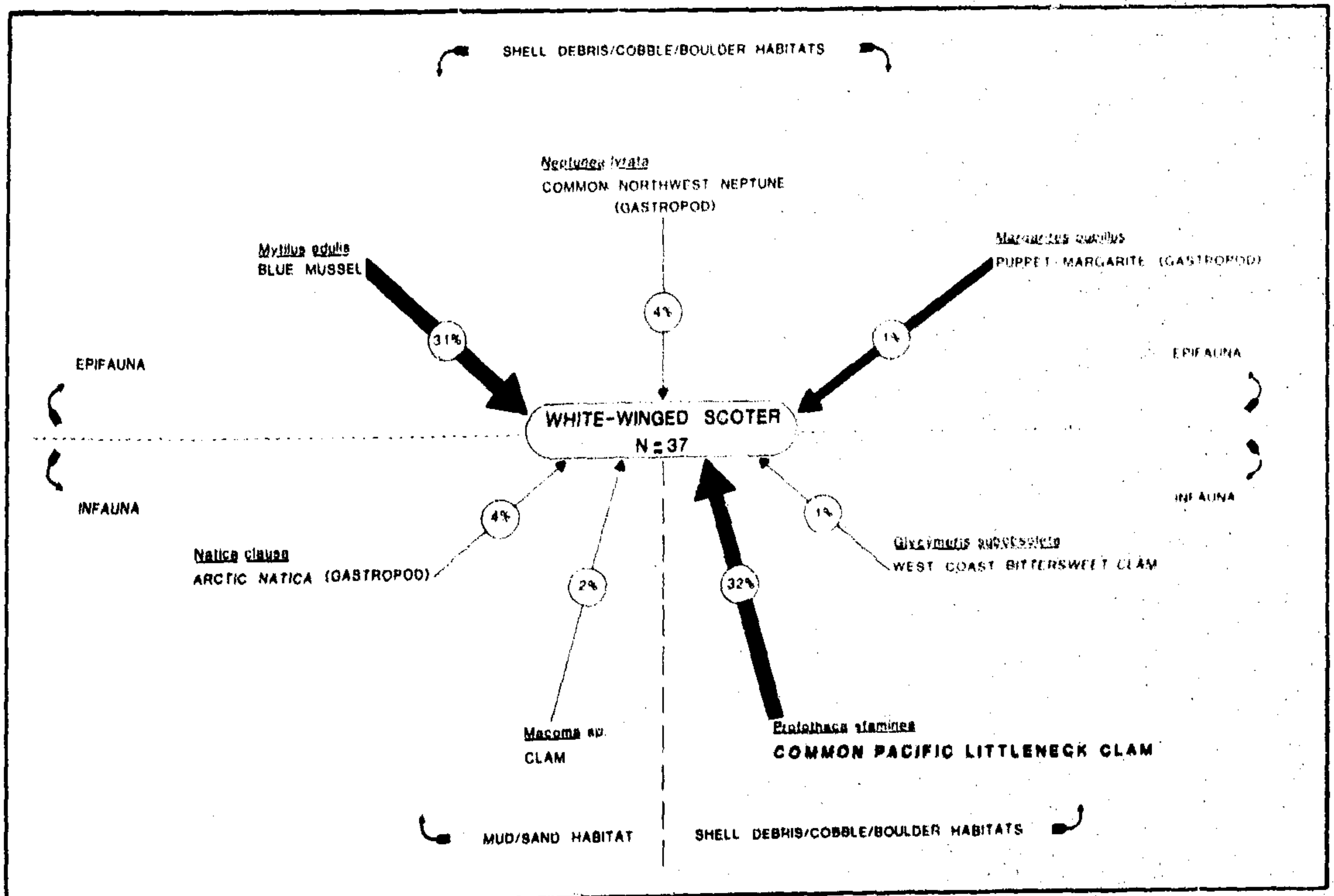
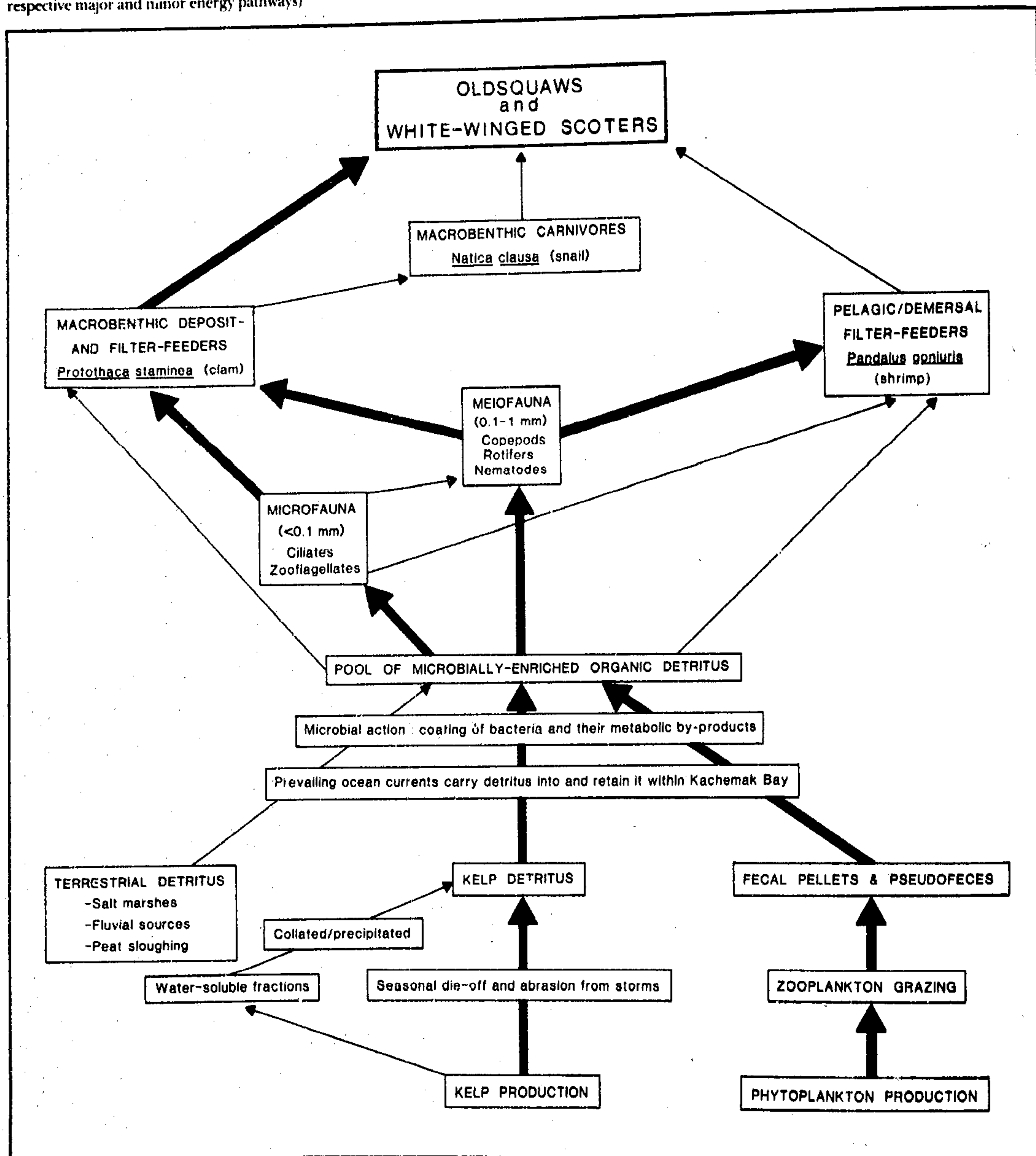


Figure 4
Hypothesized trophic relationships and environmental processes in the ecosystem of waterfowl wintering on Kachemak Bay. (Representative prey species indicated where possible, and large and small arrows show respective major and minor energy pathways)



Both sea ducks ate blue mussels and common Pacific littleneck clams. Although these species were major prey of scoters, they were of only minor importance to Oldsquaws. Moreover, lengths of these prey were markedly different for the two birds. Blue mussels ($n = 432$) from the Oldsquaws were all less than 10 mm, whereas the three from the scoters were 50–69 mm. Similarly, the 19 common littleneck clams from the Oldsquaws were less than 10 mm, whereas the 4 from the scoters ranged from 10 to 49 mm. Differences in average lengths of all prey (cf. sections 6.1.2. and 7.1.2.) were highly significant between the two species (99% level, as measured by a t-test of the differences between two means).

9. Trophic levels between primary production and seabirds

The classical view of primary production in the sea emphasizes the role of phytoplankton in the water column (e.g. Sieburth and Jensen 1970, Strickland 1970, Steele 1974). Larrance and Chester (in press) believe that the production of fecal pellets from zooplankton grazing on phytoplankton is the main source of organic detritus reaching the floor of outer Kachemak Bay in spring and summer.

However, recent work elsewhere (Tenore 1977, Mills 1975, Sieburth and Jensen 1970, Strickland 1970) has shown that organic detritus from other sources may also play a major role in driving coastal marine ecosystems. Lees and Driskell (1981) contend that abrasion of laminarian and fucoid kelps around the southern end of the Kenai Peninsula and in Kachemak Bay provides the major source of detritus. Water soluble organic fractions from kelp may also contribute to detritus (Lees and Driskell 1981, Sieburth 1968, Sieburth and Jensen 1970). Other sources of organic detritus in the bay are of terrestrial origin from streams, from salt marshes bordering the bay (J. H. Crow, unpubl. data), and from peat and coal sloughing directly into the bay along the north shore (M.P. Wennkens, pers. commun.).

Most prey of Oldsquaws and White-winged Scoters are deposit or filter feeders (Lees and Driskell 1981, Feder and Paul 1981), and, as such, they use organic detritus and its bacterial coating and associated microfauna (Tenore 1977) for food. Thus, the birds' food supply is closely linked to the existence and production of organic detritus. Although the relative importance in the ecosystem of Kachemak Bay of phytoplankton productivity and organic detritus from its various sources is unclear, lower trophic levels of the food web could be similar to detrital food chains in other coastal marine ecosystems (Tenore 1977); i.e. organic detritus — microbenthos (animals <0.1 mm) — meiobenthos (animals 0.1–1.0 mm) — macrobenthos (animals >1 mm) — fish.

In Kachemak Bay, starfish are apex predators along with fish and birds (Lees and Driskell 1981). However, the exact trophic level(s) at which apex predators feed is unknown because the nature of the microbenthos and meiobenthos are virtually unknown (Robert Griffiths, pers. commun.). The filter- and deposit-feeding prey of the birds could feed on any of these animals, and also directly ingest the bacterially-enriched detritus. Thus, depending on which of these links are present in the food web of Kachemak Bay, Oldsquaws and scoters function as first- to fourth-order carnivores. For example, when Oldsquaws eat humpy shrimp (*Pandalus goniurus*) that eat detritus, the Oldsquaws are first-order carnivores. When White-winged Scoters eat

Natica clausa snails, that eat clams, that eat meiofauna, that eat microfauna, that eat detritus, the scoters are fourth-order carnivores.

With these points in mind, the possible environmental processes and trophic relationships in the ecosystem of birds wintering in Kachemak Bay (Fig. 4) may be summarized as follows:

1. Stocks of kelp in Kachemak Bay and around the southern end of the Kenai Peninsula grow intensively in spring and summer, when phytoplankton in the area also blooms intensively.
2. Fecal pellets from zooplankton and the abrasion and seasonal die-off of kelp both produce organic detritus.
3. Currents carry the kelp detritus from the southern end of the Kenai Peninsula into Kachemak Bay.
4. Bacteria colonize the detritus at some point.
5. The microbially-enriched detritus supports a rich community of deposit- and filter-feeding demersal and benthic fauna, probably by means of one or two trophic links (micro- and meiofauna).
6. The deposit- and filter-feeding animals, in turn, support marine birds and other apex predators.

10. General discussion

Oldsquaws and scoters were collected in water depths between 2 and 20 m. We do not know precisely the depths at which the birds fed, but it is likely that White-winged Scoters collected in the outer bay fed mostly at depths shallower than those studied by Feder and Paul (1981) (ca. 29 m) and by Driskell and Lees (1977) (ca. 12–65 m), and deeper than the intertidal areas studied by Lees and Driskell (1981). Feeding depths of Oldsquaws collected in the inner bay likely overlapped the 1.5–11.3-m depths surveyed by Lees and Driskell (1981).

The presence of blue mussels, an intertidal species, in both Oldsquaws and White-winged Scoters indicates that both ducks fed at least part of the time over intertidal areas at high tide, whereas the absence of the horse mussel (*Modiolus modiolus*), an exclusively subtidal species, from their diets suggests that they may not have foraged over rocky areas when they fed subtidally. Horse mussels are abundant in the outer bay off Homer Spit, and off Bluff Point (Lees and Driskell 1981), where we collected many of the scoters. Mussels from Bluff Point, however, range in length from 75 to 150 mm (Driskell and Lees 1977), which may have been too large for the scoters.

Oldsquaws and White-winged Scoters from Kachemak Bay ate the same general taxa of prey reported from other areas (e.g. Vermeer and Bourne, this volume, Stott and Olson 1973, Nilsson 1972, Madsen 1954, Cottam 1939), both species eat mostly bivalves, gastropods, and crustaceans. However, knowledge of the availability of the birds' prey species relative to the availability of other potential prey in Kachemak Bay is sketchy. There is some similarity between the Oldsquaws' diet and benthic fauna reported from surveys in the inner bay (Lees and Driskell 1981). Animals present in the non-quantitative surveys that were also present in the Oldsquaws' diet included turrid gastropods (*Oenopota* sp.), blue mussels, *Nuculana* and *Macoma* clams, and sandlance. Dominant benthic species on rocky substrates between 4 and 16 m during SCU'BA diving surveys along the north shore of the outer bay (Lees and Driskell 1981) included the horse mussel, matting polychaete *Potamilla*, butter clam *Saxidomus* sp., green sea

urchin (*Strongylocentrotus droebachiensis*), and common northwest neptune (gastropod) (*Neptunea lyrata*). Of these, only the neptune was moderately important to White-winged Scoters, and the green sea urchin was of minor importance; the others were absent from the scoters' diet.

The general contrast between the birds' diets and the fauna identified from benthic surveys suggests that there may be differences between the kinds of animals present in the birds' feeding habitats and the areas surveyed. It is also possible that the surveys missed components of the birds' diets, and that the birds selected prey in different proportions to their occurrence in nature. In view of the size range of horse mussels off of Homer Spit (15–130 mm, Lees and Driskell 1981), the absence of smaller individuals in the diet of the scoters is puzzling.

Amounts of food in the birds ranged up to 3–4% of their net body weight; similar data on other waterfowl appear to be lacking. Despite this seeming paucity of food, however, body weights reflected a healthy condition of the birds (Sanger and Jones 1982). Also, rapid digestion rates (van Koersveld 1950) and frequent small feedings are indicated.

11. Acknowledgements

A. Fukuyama, A. DeGange, R. Gill, M. Petersen, and D. Nysewander, US Fish and Wildlife Service, assisted with field work. We thank L. Flagg, D. Hardy, and C. Larson, Alaska Department of Fish and Game, for hospitality and logistics support in Homer.

Stomach contents were processed and identified by D. Wiswar (scoters) and A. Fukuyama (Oldsquaws). G. Mueller and staff, Marine Sorting Center, University of Alaska, were particularly helpful with identifications. They and other specialists who helped were: J. Blackburn, fishes; K. Coyle, crustaceans; W. Driskell, gastropods; N. Foster, gastropods and pelycypods; K. Frost and L. Lowry, fish otoliths; H. Jones, polychaetes; H. Kajimura, fish bones; G. McDonald, nudibranch gastropods; and, G. Mueller, bryozoans, crustaceans, ophiuroids, and polychaetes.

Discussions and correspondence with P. Arneson, D. Erikson, R. Griffiths, and D. Lees on Kachemak Bay and its biota were very helpful. D. Amos, D. Wiswar, and T. Martinson assisted with data analyses and/or graphics. D. Amos, A. Fukuyama, D. Derksen, L. Krasnow, D. Lees, C. Lensink, M. Petersen, S. Peterson, P. Springer, and D. Wiswar commented on various drafts of this paper.

This study was supported by the Bureau of Land Management (BLM) through interagency agreement with the National Oceanic and Atmospheric Administration (NOAA), under which a multi-year program responding to needs of petroleum development of the Alaskan continental shelf is managed by the Outer Continental Shelf Environmental Assessment Program (OCSEAP) Office, Juneau.

12. Literature cited

Abbott, R.T. 1974. American seashells, the marine mollusca of the Atlantic and Pacific coasts of North America. 2nd ed. Van Nostrand Reinhold Co. New York. 663 pp.

Butler, T.H. 1980. Shrimps of the Pacific coast of Canada. Can. Dep. Fish. Oceans Bull. 202. 280 pp.

Burbank, D.C. 1977. Circulation studies in Kachemak Bay and lower Cook Inlet. Vol. III in Trasky, L.L.; Flagg, L.; Burbank, D.C. eds. Environmental studies of Kachemak Bay and lower Cook Inlet. Processed Rep. Alaska Dep. Fish and Game. Anchorage. 207 pp.

Cohen, J.E. 1978. Food webs and niche space. Monogr. Popul. Biol. 11. Princeton Univ. Press. Princeton, N.J. 189 pp.

Cottam, C. 1939. Food habits of North American diving ducks. U.S. Dep. Agric. Tech. Bull. 643. 140 pp.

Driskell, W.; Lees, D. 1977. Benthic reconnaissance of Kachemak Bay, Alaska. Vol. II in Trasky, L.L.; Flagg, L.; Burbank, D.C. eds. Environmental studies of Kachemak Bay and lower Cook Inlet. Processed Rep. Alaska Dep. Fish and Game. Anchorage. 102 pp.

Erikson, D. 1977. Distribution, abundance, migration, and breeding locations of marine birds in lower Cook Inlet, Alaska, 1976. Vol. VIII in Trasky, L.L.; Flagg, L.B.; Burbank, D.C. eds. Environmental studies of Kachemak Bay and lower Cook Inlet. Processed Rep. Alaska Dep. Fish and Game. Anchorage. 182 pp.

Feder, H.M.; Paul, A.J. 1981. Distribution, abundance, community structure and trophic relationships of the nearshore benthos of Cook Inlet. Pages 45–355 in Environmental assessment of the Alaskan continental shelf. NOAA/BLM, Outer Cont. Shelf Environ. Assess. Program. Boulder, Colo. Final Rep. Vol. 14. 676 pp.

Keen, A.M.; Coan, E. 1974. Marine molluscan genera of western North America, an illustrated key. 2nd ed. Stanford Univ. Press. 208 pp.

Larrance, J.D.; Chester, A.J. In press. Source, composition, and flux of organic detritus in lower Cook Inlet. In Environmental assessment of the Alaskan continental shelf. NOAA/BLM, Outer Cont. Shelf Environ. Assess. Program. Boulder, Colo. Final Rep.

Lees, D.C.; Driskell, W.B. 1981. Investigations on shallow subtidal habitats and assemblages in lower Cook Inlet, Alaska. Pages 419–610 in Environmental assessment of the Alaskan continental shelf. NOAA/BLM, Outer Cont. Shelf Environ. Assess. Program. Boulder, Colo. Final Rep. Vol. 14. 676 pp.

Madsen, F.J. 1954. On the food habits of the diving ducks in Denmark. Danish Rev. Game Biol. 2:157–266.

Martin, A.C.; Gensch, R.H.; Brown, C.P. 1946. Alternative methods in upland gamebird food analysis. J. Wildl. Manage. 10:8–12.

Meyer, T.L.; Cooper, R.A.; Langton, R.W. 1979. Relative abundance, behaviour, and food habits of the American sandlance, *Ammodytes americanus*, from the Gulf of Maine. Fish. Bull. 77:243–253.

Mills, E.L. 1975. Benthic organisms and the structure of marine ecosystems. J. Fish Res. Board Can. 32:1657–1663.

Nilsson, L. 1972. Habitat selection, food choice and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season. Ornis Scand. 3:55–78.

Peterson, S.R.; Ellarson, R.S. 1977. Food habits of Oldsquaws wintering on Lake Michigan. Wilson Bull. 89:81–91.

Pinkas, L.; Oliphant, M.S.; Iverson, I.L.K. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish and Game, Fish. Bull. 152:1–105.

Robins, C.R.; Bailey, R.M.; Bond, C.E.; Brooker, J.R.; Lachner, E.A.; Lea, R.N.; Scott, W.B. 1980. A list of common and scientific names of fishes from the United States and Canada. 4th ed. Am. Fish. Soc. Spec. Publ. No. 12. 174 pp.

Sanger, G.A.; Jones, R.D., Jr. 1982. The winter feeding ecology and trophic relationships of marine birds in Kachemak Bay, Alaska. Pages 161–294 in Environmental Assessment of the Alaskan continental shelf. NOAA/BLM, Outer Cont. Shelf Environ. Assess. Program. Boulder, Colo. Final Rep. Vol. 16. 603 pp.

Science Applications, Inc. (SAI). 1979. Lower Cook Inlet interim synthesis report. NOAA/BLM, Outer Cont. Shelf Environ. Assess. Program. Boulder, Colo. 241 pp.

Sieburth, J.M. 1968. The influence of algal antibiosis on the ecology of marine microorganisms. Pages 63–74 in Droop, M.R.; Wood, E.J.F. eds. Advances in microbiology of the sea. Acad. Press. London and New York.

Sieburth, J.M.; Jensen, A. 1970. Production and transformation of extra-cellular organic matter from littoral marine algae: A résumé. Pages 203-223 in Hood, D.W. ed. Organic matter in natural waters. Univ. Alaska. Inst. Nat. Sci. Fairbanks. Occas. Publ. No. 1.

Steele, J.H. 1974. The structure of marine ecosystems. Harvard Univ. Press. Cambridge, Mass. 128 pp.

Stott, R.S.; Olson, D.P. 1973. Food-habitat relationships of sea ducks on the New Hampshire coastline. *Ecology* 54:996-1007.

Strickland, J.D.H. 1970. Introduction to recycling of organic matter. Pages 3-5 in Steele, J.H. ed. Marine food chains. Univ. Calif. Press. Berkeley. 552 pp.

Swanson, G.A.; Krapu, G.L.; Bartonek, J.C.; Serie, J.R.; Johnson, D.H. 1974. Advantages in mathematically weighting waterfowl food habits data. *J. Wildl. Manage.* 38:302-307.

Tenore, K.R. 1977. Food chain pathways in detrital feeding benthic communities: A review, with new observations on sediment resuspension and detrital recycling. Pages 37-53 in Coull, B.C. ed. Ecology of marine benthos. Belle W. Baruch Library Mar. Sci. 6. Univ. South Carolina Press. Columbia.

Trasky, L.L.; Flagg, L.B.; Burbank, D.C. 1977. Impact of oil on the Kachemak environment. Vol. I in Trasky, L.L.; Flagg, L.B.; and Burbank, D.C. eds. Environmental studies of Kachemak Bay and lower Cook Inlet. Processed Rep. Alaska Dep. Fish and Game. Anchorage. 123 pp.

van Koersveld, E. 1950. Difficulties in stomach analysis. Pages 592-594 in Proc. Xth Int. Ornithol. Congr. Almqvist and Wiksells Boktryckeri AB. Uppsala. Stockholm.

Vermeer, K.; Bourne, N. This volume. The White-winged Scoter diet in British Columbia waters: resource partitioning with other scoters.

Welty, J.C. 1962. The life of birds. Saunders. Philadelphia and London. 546 pp.